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THE DISTRIBUTION OF INSECTS IN WESTERN NORTH AMERICA.*

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The fauna of the western part of North America has long been recognized as possessing many characteristics which have differentiated it from that found elsewhere in North America. This is particularly the case as regards the insects and Le Conte† as early as 1859 called attention to this. Other entomologists in more recent years have mentioned this fact and have cited many cases to show its peculiarity. The insect fauna as a whole, however, has not been studied in regard to this point, in the manner that it has merited.

Many years ago, I became interested in the subject and I have kept up my interest ever since and have availed myself of all opportunities that would enable me to gain information bearing upon it. I have studied all orders of insects to a certain extent, but most of my conclusions have been based upon a close study of the Coleoptera, particularly of the wingless and less mobile groups, such as certain of the *Carabidæ*, the *Silphidæ*, the *Tenebrionidæ*, the *Otiorychinæ*, and so forth. The other Coleoptera were used as checks as were in fact other groups of insects, and all other information bearing upon the subject of distribution in the territory under study, freely drawn upon for purposes of guidance.

* A revision of the paper read August 5, 1915, at the University of California, before the Summer Meeting of the Entomological Society of America.

† The Coleoptera of Kansas and Eastern New Mexico, by John L. LeConte, M. D., Smith. Miss. Contrib. to Knowledge, Vol. XI (1859).

As a result of these studies, I have come to believe that though the West Coast fauna is to a degree complex, it is yet made up of a definite number of elements which can be distinctly separated. The insect fauna as we now know it, has been derived from older faunas and these were either northern or southern in their origin. Each of these primary portions was in its turn composed of elements which had come into their present territory at different times and along different roads. Certain of these had remained pure and are at present restricted to definite areas, while others had either wholly or partially invaded regions already occupied by other elements and become mixed with them. These facts are of course in general in

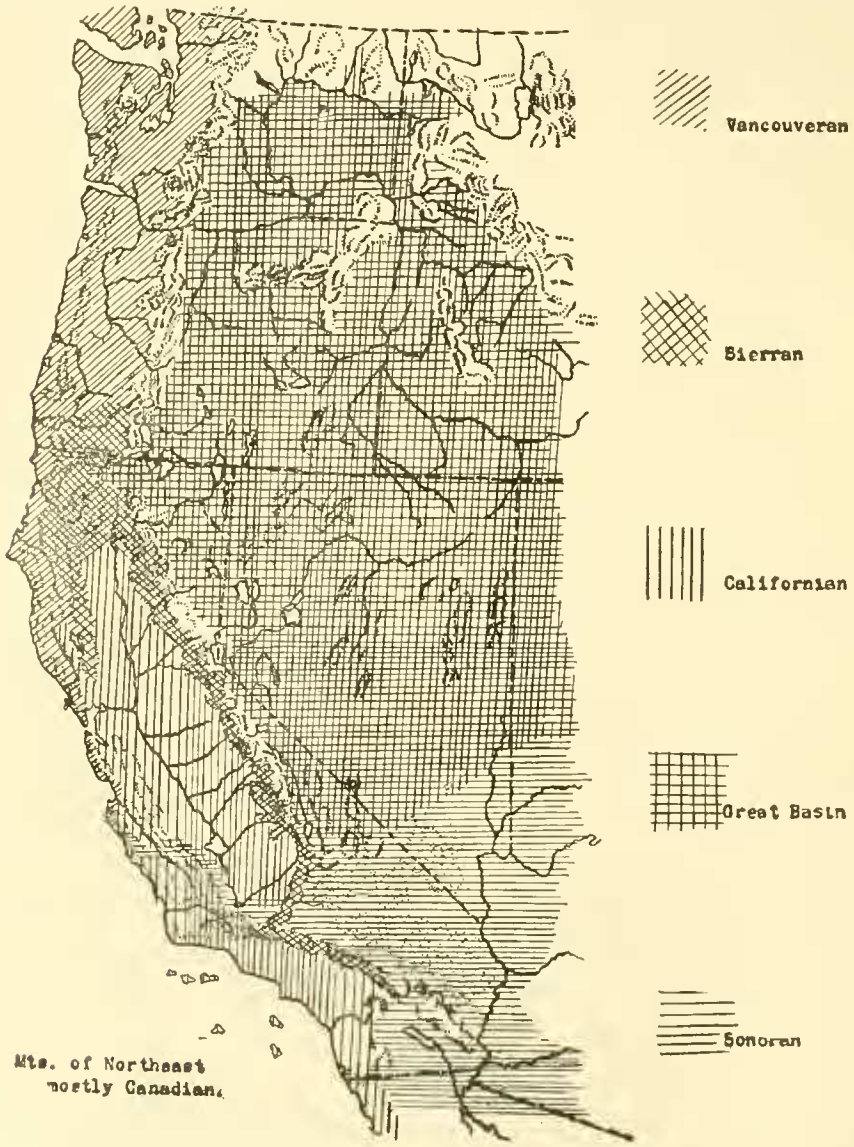

Fig. 1. Map showing the Faunal Areas of the Pacific States of North America.

keeping with those worked out by Merriam* and other mammalogists and ornithologists and substantiated by the botanists. Certain of the detailed results secured have, however, been found to be at variance with those found by others or to have previously not been worked out.

In general the insects which are considered to be of northern origin now occupy the northern and more mountainous portion of the territory. The greater portion of this, such as that including the lower levels of the Aleutian Islands, particularly the eastern ones, the southern margin of the Alaska Peninsula, southeastern Alaska, the western part of British Columbia as from the Selkirks west, Washington and Oregon west of the Cascade Mountains, and the wet and cool coastal strip of California, extending as far south as middle Monterey County, now supports a fauna which I have called the Vancouveran. The name Transitional as applied to this fauna, though generally used by previous workers, I consider misleading. The fauna is a pure one, in fact one of the purest in North America. It contains many peculiar groups of insects, some almost in their entirety, and is especially rich in such families as the *Carabidæ*, *Staphylinidæ*, *Elateridæ* and certain groups which are more or less closely associated with the coniferous forests. The following are good representatives: the genus Omus, the subgenus *Brennus* of *Scaphinotus*, the impunctate division of *Pterostichus*, *Zacotus*, *Metrius*, *Promecognathus* and the American representatives of *Trigonurus*. *Rosalia funebris* Mots. is also a characteristic member of this fauna, but it extends considerably beyond its confines. The fauna has existed in approximately its present territory from the Tertiary period and no doubt from well back in that period, being in fact a Tertiary fauna which has come down to us in a pure state. Many of the species that it contains have probably not changed during this long series of years but others have, some having become broken up into races which, becoming more and more isolated, have formed new species, subspecies, and so forth. As a result, the fauna is not the same throughout its extent. It gradually divides itself up into several subfaunas.

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* The Geographical Distribution of Life in North America with Special Reference to Mammalia, by C. Hart Merriam, Proceed. Biol. Soc. Wash. Vol. VII, April 13, 1892.

The first of these occupies the following regions: the coastal belt of southeast Alaska and British Columbia with the adjacent islands, the Puget Sound Basin of Washington and the Willamette Valley of Oregon, and extends fully up to the five thousand foot level on the Cascades. This contains the Vancouveran fauna in its purest form and with its species but little modified throughout its extent. Characteristic Coleoptera of this area are *Omus dejeani* Reiche, *Cychrus tuberculatus* Harr., *Carabus taedatus* Fab., in its typical form, *Nebria mannerheimii* Fisch., *Pterostichus herculaneus* Mann. and *Pterostichus validus* Dej., and *Miscodera insignis* Mann.

Next we have a subfauna that might be called the Pacific Maritime. This occupies that very wet region to the west of the Olympic and Coast Ranges of Washington and with secondary modifications taking place chiefly in northwestern Oregon, in southwestern Oregon and northwestern California, in Mendocino County, California, and south of the Russian River in California, extends down the coast as far as middle Monterey County, California. Within this maritime area, the fauna as far as the species are concerned, is quite similar to that found in the pure Vancouveran, but the form and appearance of many of the species has changed. Melanism is markedly evident here and is to be noted in such widely separated families as the *Carabidæ*, the *Elateridæ*, the *Cantharidæ* (*Lampyridæ*), the *Scarabaeidæ*, and the *Rhynchophora*. Increase in size is also to be noted with regard to many of the species. To illustrate this, I will cite but a few examples. In the *Carabidæ*, in the genus *Scaphinotus*, we have the species *S. angulatus* Harr. which is of a metallic purple color in those specimens dwelling in the Puget Sound Basin and the Willamette Valley, and absolutely black in those which are found in the wet coast belt, though otherwise unmodified. In southwestern Oregon and northwestern California, a related but distinctly different species, *S. behrensi* Roesck, is found replacing the above. *Scaphinotus angusticollis* Fisch. in the pure Vancouveran region from southeastern Alaska to the eastern side of the Willamette Valley, is typically of a ferruginous color. West of the Olympics and Coast Range of Washington and the Willamette river in Oregon, it is absolutely black. In Washington, it is structurally the same as the typical form; in western Oregon, larger and with

the alternate elytral intervals more reduced or irregular; in southwestern Oregon and northwestern California, it occurs with a more angulate prothorax, still more modified elytra, and with the male tarsi somewhat changed; while in the southern part of its range, in Mendocino and northern Sonoma County, California, it appears as a much larger insect and much modified in every regard. In *Pterostichus amethystinus* Dej. we have a species with bluish elytra which extends from Alaska to middle Mendocino County, California. South of this, it is replaced by *P. scutellaris* Lec., a species which has absolutely the same habitat and only differs from the preceding by being all black. It extends into Monterey County, California. Among the *Elateridæ*, we have numbers of species which like *Athous ferruginosus* Esch., have a black phase within the southern maritime area. In the genus Silis, the species and varieties found along the coast and in the high mountains of the Pacific Coast are mostly black, whereas in the interior lowlands they are yellow. Among the *Rhynchophora*, we have one, *Rhynchites bicolor* Fab., one of the most widely distributed weevils in North America which has its only known black phase in the middle coastal belt of Oregon.

A second and more greatly modified portion of the Vancouveran fauna is that which inhabits a strip of country that starts in the west central part of Oregon, runs south and southeast, including all of the moderately elevated mountains in Southern Oregon and Northern California, and extends along the western flanks of the southern Cascades and Sierras into Southern California and with breaks, also into the San Pedro Matir of Lower California. This subfauna I would call the Sierran. It occupies much of the same country as that covered by the western yellow pine, and though it receives many species from those faunas found immediately above and below it, is in no sense a transitional one as often called. It is a distinct subfauna and a direct offshoot of the Vancouveran. Its species are almost always either like those to be found in the pure Vancouveran or are derivatives of the same. In the northern area of the Sierran subfauna, certain species show a strong tendency to break up into many weak races which are more or less limited to various small areas. This unstableness is no doubt partly due to climatic and partly to topographical conditions, for the country is much broken up, there being many

small ranges with variously exposed slopes. In the region extending from Mt. Shasta south to the American river, some of the offshoots of the primitive species have segregated themselves into rather distinct species and subspecies, serving thereby to define this as a rather distinct subregion and one with a fairly well defined secondary fauna. In the territory running from the American river south to the Merced river, we find marked off in a similar way another secondary faunal area; in the southern Sierras, quite another; while in the San Bernardino Mts. there is still another. These secondary faunas, though not well defined by the majority of the Sierran species, are yet very distinctly outlined by others, as for instance, by certain species of *Omus*, *Scaphinotus*, *Pterostichus* and *Pleocoma*.

Two of the North American faunas most closely related to the Vancouveran and two, which like it, are most likely remnants of the same northern Tertiary fauna, are one small fauna confined to parts of the mountains of western Idaho, the Coeur d'Alene and Moscow; and the fauna of the upper levels of the southern Appalachian mountains, the so-called Alleghanian. These two are relict and endemic faunas and possess as would be expected, many species or related species in common. In the Idaho fauna, we have certain species like *Pterostichus sphodrinus* Lec. which are closely related to those found in the Vancouveran like *Pterostichus ovicollis* Schaef.; and others as *Scaphinotus relictus* Horn and *H. merkeli* Horn that have their nearest relatives in *Scaphinotus imperfectus* Horn, *S. debilis* Lec. and *S. incompletus* Schz. of the southern Alleghanies. In *Pterostichus* we have a peculiar and small group of species that have more or less prognathous mandibles and are quite subterranean in habit. On the Pacific Coast we have three, *P. caligans* Horn, being the best known, one in Idaho, and *P. grandiceps* Ch. and *P. rostratus* Neum. in the Appalachian Mountains. All of the above mentioned species are so highly specialized that they cannot be anything but relicts. They could not possibly have migrated to their present abode subsequent to the Glacial Period, though like the last mentioned, they might have extended their territory.

In the Cascades and Sierras, at elevations immediately above those occupied by the Vancouveran and its offshoot, the Sierran, we have a fauna that is more alpine in its nature.

The lower belt of that fauna, that found within the fir zone, is generally spoken of as the Canadian, that immediately above it and in the more barren treeless areas as the Hudsonian, and that on the tops of the high peaks as the Arctic. These faunas are in reality marginal or fringing faunas. They fringe the snow fields of the mountains and the barren wastes of the north, advancing and retreating with them, and have done so not only during the present period, but undoubtedly during the entire portion of the Great Ice Age, and I believe even before that were only to be found in the cooler areas of the north. During the period of greatest ice development, the Pleistocene, they were driven down to the lower levels and forced much farther south than they were before. With the decline of this period, they retreated both upwards and northward. At the more southern limits of their distribution their retreat was often prevented by breaks in the ranges or by the lowness of the mountains so that their continuity was interrupted leaving as we find today little islands of fauna here and there restricted to the more elevated parts of the high mountains.

The first of these, the Canadian, is in the west almost entirely a forest loving fauna. Where it comes in contact with the Vancouveran and Sierran, it blends to some extent with them and as a result is often hard to separate. It has also borrowed many species from these as they have from it. It commences in the north as a continuation on to the mountains of that extensive lowland fauna which populates the vast areas of western Canada. Then it continues south along the mountains, at first as a rather broad belt, later as a much narrower one, and wedged in between the Vancouveran and Sierran, and the Hudsonian on the west slopes; and the Great Basin fauna, a portion of the so-called Upper Sonoran, and the Hudsonian when the mountains are sufficiently high for that, on the east side. Its forest types of Coleoptera are fairly characteristic, such as many of its *Elateridæ* and *Cerambycidæ*, but its *Carabidæ* are less so. *Pterostichus protractus* Lec. and *Platynus bogemanni* Gyll. are, however, quite distinctive of it in the more southern Cascades and the Sierras.

The Hudsonian is in most places a very narrow zone, but it is very distinct. In Alaska, it is found on the uplands of the Aleutian Islands, on the mountains and the north side of the Alaska Peninsula, to quite an extent about the Kenai Peninsula,

and thence south along the flanks of the ranges which fringe the Coast. In British Columbia it is more inland and on the higher mountains and it continues as such along the Cascades of Washington and Oregon and the Sierras of California, but gradually ascends as it extends southwards. In the Cascades, as on Mt. Rainier, it is found at about seven thousand feet, on Mt. Shasta at eight thousand, in the Lake Tahoe region near nine thousand, while in the southern Sierras it is well above ten thousand feet. A few of its more widely distributed and characteristic beetles are *Nebria sahlbergi* Fisch., *Bembidium incertum* Mots., *Amara erratica* Sturm, and *Cryptohypnus bicolor* Esch. Besides these, there are certain others which are only to be found in the mountains of the West but which, because of certain peculiarities of distribution throw so much light upon the problem that they are worthy of being especially mentioned. Such is *Nebria trifaria* Lec. a large and very attractive black species. This is undoubtedly a glacial relict, for it is now only to be found high up near the snow fields on the Olympic Range, Mt. Rainier and Mt. Jefferson of the Cascades, and the Rockies of Colorado. The rare *N. ingens* Horn of the high southern Sierras, which differs from the preceding chiefly in having very much rounded humeri and atrophied wings, is, I am convinced, but a degenerate offshoot of the preceding which was forced south and later entirely separated from the parent stock. *Nebria ovipennis* Lec. and its three associated species are also of importance from the same viewpoint. They are all of moderate size, entirely apterous, and with elliptical elytra, hence extremely specialized and dependent upon their particular environment. The most northern, *N. kincaidi* Schw., an entirely metallic species of a purplish copper color, has been found close to the coast at Farragut Bay, Alaska, and near the snow fields on Glacier Peak and Mt. Rainier, Washington. A second, *N. columbiana* Casey, which resembles the preceding, but has only the elytra metallic, was described from British Columbia, but has also been found on Glacier Peak and Mt. Rainier, Washington, and Mt. Jefferson, Oregon. The third, *N. ovipennis* Lec., which is but an offshoot of the preceding and differs only in color, being entirely brownish or piceous, in other words more heavily pigmented, is to be found on the higher peaks of the Lake Tahoe region in California and above 10,500 feet in the southern

Sierras. The fourth species, *N. diversa* Lec. is of a yellowish color and is confined to the sea coasts of Washington and Oregon. The only close relatives that these four have are certain species found in the more eastern part of the Himalayas and in northeastern Asia. The last beetle to be mentioned in this connection shows another peculiarity of distribution due to the retreating ice. This is *Pterostichus brunneus* Dej., a species first described from Sitka on Baranoff Island, later found on Orcus Island near the mouth of Puget Sound and no doubt occurring on other islands in the same general region, and on the mainland only high up near the timber line as in the Selkirks of British Columbia, on Glacier Peak and Mt. Rainier in Washington, and on Mt. Jefferson in Oregon. On the islands, it was left stranded, but by adaptation was able to persist, while on the mainland it could preserve its natural environment by merely retreating with the ice to the higher levels.

The faunas of southern origin are to be found in their purest state only in the more southern part of our territory though derivatives of the same do in certain regions extend quite far to the northward. The best known of these is the Sonoran which, when considered in its strictest sense, may be said to occupy all those hot and more or less barren uplands in northern Mexico and the semi deserts and drier regions of our own Southwest, with extensions into western Texas, southern New Mexico and Arizona, and the more desert parts of southeastern California. The fauna of the Colorado Desert as well as that of its more upland extension, the Mojave Desert, is typically Sonoran. Certain elements of this also extend more westward along our southern border to the coast at San Diego and from the Mojave through the hot Walker Basin into the southern San Joaquin Valley. Here it is to be found mainly on the west side of the valley as in western Kern County and in an attenuated form in southern Monterey County. Some of its most characteristic beetles are among the wingless *Tenebrionidæ*, such as in the genera *Edrotes*, *Triorophus*, *Zopherus* and *Asida*, and in the wingless *Otiorychinæ* like *Ophrastes* and *Eupagoderes*, and the genus *Monilema* of the *Cerambycidæ*.

A derivative of the Sonoran fauna which is generally spoken of as the upper Sonoran, though it is more accurately defined as the Great Basin fauna, extends throughout the entire area

between the Rocky Mountains and the Sierra Nevadas, and thus includes northern Arizona, California east of the Sierras, Nevada, eastern Oregon and eastern Washington, Utah, parts of Wyoming, the lowlands of Idaho, and reaches its northern limit in the Okanagan Valley in eastern British Columbia. Certain portions of this fauna also break through the mountain barriers on the west and thus extend themselves. South of Mt. Whitney a portion passes through the Walker Basin in company with the more typical Sonoran and extends into the San Joaquin Valley. Another portion runs westward from Modoc and Lassen Counties and passing north of Mt. Shasta, invades the northwestern part of Siskiyou County. The insects of this fauna are generally derivatives of the true Sonoran so not sharply differentiated. The *jejunas* group of the genus *Platynus*, *Agrilus walsinghami* Cr., and the hairy group of *Eleodes* are perhaps as characteristic as are any Coleoptera that we have in the subfauna.

That other southern fauna, the one which comprises the greater portion of the insect population of the southern part of California, is not a derivative of the present Sonoran. It is a fauna which has come to us directly from the south through Lower California and presumably in earlier times from lands farther to the south. It is very old and very distinct, having many genera and the bulk of its species totally different from those of the Sonoran. It came into California long before the Sonoran did and consequently is more thoroughly established in southern and middle California. The species are now some of the most characteristic within the state and the fauna as a whole is so dominantly Californian that it might be called the Californian fauna. It is now to be found not only throughout all of Southern California west of the San Bernardino and Sierra Madre Ranges, but along the coast to San Francisco, throughout the more southern portion of the Coast Range, and the greater part of the San Joaquin and Sacramento Valleys, extending as far north as Shasta County. In the drier parts of the state, it is therefore even more dominant than the Sonoran and it sends many of its characteristic forms well within that claimed by the Vancouveran and Sierran as in the foothill regions of the more northern Coast Range and the Sierra Nevada itself, thus sharing equally with the faunas of northern origin, the possession of the land. At one time, the

northern species extended much farther south than at present and in general were more in evidence in the south than now, but within recent times they have undoubtedly both retreated and decreased in numbers in the southern areas. The southern forms have, on the contrary, been doing the opposite so that they have gradually supplanted the preceding. This, therefore, accounts for the fact that there are islands of northern forms within the territory occupied by southern forms. Wherever southern forms have run north, they are always to be found connected with their basic stock in the south, no matter how far north they have gone and no matter at what time they advanced. Some of the characteristic species of the Californian fauna are the members of the *dilatatus* group of *Anisodactylus* in the *Carabidæ; Dystaxia*, *Schizopus* and *Glyptoscelimorpha*, in the *Buprestidæ; Ipochus fasciatus* Lec. in the *Cerambycidæ; Phloeodes*, *Coelus*, *Eulabis*, *Nycotporis*, *Cibdelis* and *Coniotis*, in *Tenebrionidæ;* and *Trigonscuta* and *Rhigopsis* in the *Otiorychinæ*.

Our west coast fauna we thus find has the bulk of its species of insects included within the very old Vancouveran fauna and the equally old Californian fauna, two faunas that are restricted to the Pacific Coast and that have passed through the Pleistocene without much injury to themselves. Supplementing these, are the several marginal faunas of the mountains and the desert faunas of the southeast. The Vancouveran, like those found in the mountains of western Idaho, and in the southern Alleghanies, is a relict fauna, a remnant of a more or less upland fauna which was widely distributed throughout the more northern parts of North America during Tertiary times. It is the largest remnant of the three and is only surpassed among similar fauna by that of the Japano-Manchurian region. The Californian is quite isolated though it shows a strong relationship to that found in the more barren parts of northern Chili and Peru. The marginal faunas on our mountains link up our territory with that to the north and northeast of us and the Sonoran does the same with regard to the country to the southeast. Certain of our peculiarities can also be indicated by considering the subject from a negative standpoint. For instance, we find that very little of the Neotropical or tropical fauna of South America, has reached us, whereas quite a noticeable amount has found its way into eastern North America. *Diabrotica soror* Lec. is one of our few derivatives

from that. We also lack the most characteristic elements of those faunas, the Austro-Riparian and Carolinian, which are such a feature of the eastern part of North America. Thus we have but a few *Scarabaeidæ* and few *Chrysomelidæ* as compared with the East; no representative of *Lucanus*, *Copris*, *Onthophagus*, *Anomala* and but few of *Phyllophaga* (*Lachnosterna*) from among the *Lamellicorns;* but a weak representation of *Melanotus*, an Elaterid genus rich in species in the eastern states; and not a single species of *Evarthrus*, *Pasimachus* and *Dicaelus* from among the Carabidæ. Hence we may say that the fauna of western North America as a whole when judged from the standpoint of its insects, is a most distinct one, yet one which can be linked with the faunas of the rest of the world.